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THE DEVELOPMENT OF THE EMBRYO SAC OF *SMILACINA STELLATA*

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(WITH PLATE XV)

The object of this paper is to describe the development of the embryo sac of *Smilacina stellata* (L.) Desf., with a view to its possible bearing on the current interpretations of the lily type of embryo sac.

In 1880 TREUB and MELLINK (27) reported that in *Lilium bulbiferum* and in *Tulipa Gesneriana* the embryo sac mother cell develops directly into the embryo sac without any previous divisions.

In 1884 GUIGNARD (11) and also STRASBURGER (24) called attention to the fact of a reduction of the number of the chromosomes during the development of the germ cells of angiosperms. STRASBURGER (25) further pointed out in 1888 that in the case of the embryo sac in certain orchids and in *Allium*, the reduction of the number of the chromosomes occurs in the nucleus of the embryo sac mother cell.

It was further established simultaneously by OVERTON (16) and GUIGNARD (12) that, in the lilies and other plants in which the embryo sac mother cell develops directly into the embryo sac without previous division, reduction takes place in the nucleus of the young embryo sac. The natural conclusion from these discoveries is that the young embryo sac in these cases is the morphological equivalent of a pollen or embryo sac mother cell. That the nuclei resulting from the first two divisions in the embryo sac of the lilies are morphological equivalents of the microspores is strongly suggested by these results.

STRASBURGER (26) in 1894, discussing the formation of the embryo sac of the lilies, concludes that the cell in which the reduction of the chromosome number takes place is to be regarded as a mother cell and not simply as a young embryo sac, since in the ovaries of *Allium* and *Helleborus* he had found that the reduction of the chromosomes takes place in the embryo sac mother cell before it has

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undergone division. He concludes that in these cases the course of development is abbreviated, so that there is no formation of reduced cells which are to be immediately absorbed, as is the case in many other species. According to this view the heterotypic and homeotypic divisions are transferred to the early stages of development of the gametophyte.

The term "macrospore" or "megaspore" is frequently loosely used by the supporters of this view in reference to the cell which develops into the embryo sac, whether it be the young embryo sac itself, or one of the daughter cells, or one of four granddaughter cells which have been formed by the reduction divisions.

From the evident homology of the nuclei of the first two divisions of the embryo sac mother cell of the lilies with the microspores, as suggested by the discoveries of GUIGNARD, STRASBURGER, OVERTON, and also later investigators, the obvious interpretation of their nature is that they are megaspores. According to this view the reduction divisions may be regarded as the sole criteria of spore formation.

STRASBURGER (26) further says, in reference to the significance of the number of divisions which intervene between the embryo sac mother cell and the completed embryo sac, with its egg: "That the number of these intervening divisions is not of primary importance is proved by the fact that the number is not always the same: thus in *Lilium* and *Tulipa* there are but three; in *Ornithogalum*, *Comelyna*, and species of *Agraphis*, there are four; in yet other cases the number is greater than five. . . ."

Smilacina stellata, the species which I have studied, is a member of the order Convallariaceae. The data as to the morphological relationships of the genus *Smilacina* are scanty and in part contradictory. The order Convallariaceae is retained by ENGLER and PRANTL under the group Asparagoideae, but the nature of the relationship of the group to the other orders of the Liliales is not very clear. The other members of the Convallariaceae whose embryo sac development has been studied are *Convallaria*, *Paris*, and *Trillium*.

Convallaria majalis has been investigated, as to the development of its embryo sac, by WIEGAND (29). He reports that the embryo sac mother cell divides to form two fully separated daughter cells, the outer of which is the larger. The nuclei of both of these cells

undergo a second division, but this time no cell walls are formed. The resulting four nuclei again divide, and the partition wall between the two sets of nuclei disintegrates enough to allow a nucleus from the lower set to pass through and unite with one from the upper set. This fusion nucleus is the endöperm nucleus. If this account is correct, we have at least a partial absorption of a cell wall in the formation of the embryo sac and the utilization of all four nuclei of the double division, as will be described below for *Smilacina stellata*.

WIEGAND'S account is contradicted, however, by SCHNIEWIND-THIES (21), who reports that in *Convallaria majalis* the mother cell divides to form a row of four cells, one of which develops into the embryo sac, while the other three disintegrate. As a possible explanation of the difference which exists between her account and WIEGAND'S, she remarks that greenhouse material rarely shows normal development. WIEGAND, however, does not mention the use of such material in his investigation. That both WIEGAND and SCHNIEWIND-THIES are correct is possible, but not very probable. It is very much to be desired that this species be reinvestigated to clear up this confusion.

ERNST (9) reported that in *Paris quadrifolia* the lower of two daughter cells develops into the embryo sac. The upper daughter nucleus divides once, but the resulting nuclei degenerate. In the same paper he reports that the lower of two daughter cells of *Trillium grandiflorum* develops into the embryo sac. The upper daughter cell is smaller from the first and rarely divides. For *T. recurvatum*, on the other hand, CHAMBERLAIN (6) has reported that the embryo sac develops from the lower of four megaspores.

Though scanty, the literature on the order Convallariaceae suffices to suggest that there exists in the group great variation in the conduct of the cells and the nuclei resulting from the reduction divisions, and that we may here find transition conditions between the so-called normal type of embryo sac formation and that found in the lily.

The materials for this study were collected in the vicinity of Beloit, Wis., in May 1906 and 1907, in November 1907, and in June 1908. Flemming's strong solution gave the best fixation for the early stages, but worked badly for mature embryo sacs. With these mature embryo sacs the following chromacetic fixative gave good results:

chromic acid 0.7^g, glacial acetic acid 0.5^{cc}, water 100^{cc}. A fixative composed of two parts absolute alcohol and one part glacial acetic acid gave very good results also. Flemming's weak solution was not tried.

Smilacina stellata is especially favorable for obtaining a complete series of stages of the early development of the embryo sac. The flowers, eight to fourteen in number, are borne in a raceme, which does not expand till the embryo sac has nearly reached the eight-celled stage. It is therefore possible to cut an entire raceme longitudinally and get a maximum number of ovules cut parallel to their long axes. The oldest flowers are at the bottom. Each flower contains five to seven ovules, and about seventy racemes were cut in paraffin.

In the material collected November 16, the nucellus was only partly developed in the lower flowers of the raceme. There were no mother cells to be distinguished in any of this material. Material collected May 7 showed, in a few shoots, mother cells in the synapsis stage in the lower flowers, while at the top of the shoot the nucellus was barely differentiated. Most of the racemes taken at this date were farther developed than those mentioned above the younger flowers being at least in the synapsis stage.

The mother cell is located at a variable depth beneath the surface of the nucellus. Not uncommonly it is immediately beneath the epidermis (*fig. 1*). In other cases it is separated from the epidermis by one cell layer. Most commonly two cell layers intervene (*fig. 2*). Measurements of several camera drawings of the mother cell at the synapsis stage gave an average breadth of 22 μ , and an average length of 30 μ .

I shall not here take up in detail the question of the reduction of the chromosomes. In the first division of the mother cell, thick double chromosomes, characteristic of the metaphases of the heterotypic division, appear (*fig. 3*). The number of bivalent chromosomes, as shown in the anaphase stage of this division, is twelve. The sporophytic number, as shown by root tip cells, is twenty-four.

A definite cell plate, and in most cases a cell wall, is formed, separating the two daughter nuclei of the first division before the second division takes place (*figs. 4, 5*). The cell plate is formed by

the thickening of the connecting fibers in the equatorial region to form a septum which separates the cells. This splits in the central region first, and often a thin layer of orange staining material is to be seen between the split layers. The plasma membranes formed by the splitting of the cell plate are made very conspicuous in cells in which there is a slight plasmolysis. The cell wall seems in most cases to be fully formed before the second division is completed. Several preparations were found in which the wall seemed to be incomplete after the second division (*fig. 7*). These, however, may represent a stage in the removal of the cell walls, as described below.

In many cases the wall of the first division is transverse, but not infrequently it is oblique (*figs. 4, 12*). The walls formed in the second division are extremely variable as to their position. Frequently (*fig. 11*) they are transverse, forming a linear row of four cells. Very often the outer daughter cell divides longitudinally and the inner transversely (*fig. 8*). Less frequently, the outer divides transversely and the inner longitudinally (*fig. 6*). *Fig. 7* shows an arrangement which is occasionally met with, both daughter cells having divided longitudinally. Rather frequently one section shows two cells divided transversely, while the next succeeding section shows two cells divided longitudinally (*figs. 9, 10*). This arrangement could only result from the division of the mother cell at first by a longitudinal wall parallel to the plane of the section, and the division of one of the daughter cells by a transverse wall and of the other by a longitudinal wall. This case is easy to recognize when the plane of the section is such that both of the cell boundaries of the second division are vertical. It is much more difficult to recognize when one of the cell boundaries of the second division lies in or near the plane of the section. Such a mode of division is of course frequently found in pollen mother cells. *Fig. 12* shows, however, by far the most common arrangement of the cells, in which the first wall is oblique and the walls of the dividing daughter nuclei are approximately at right angles to it.

Most of these various arrangements of the four cells resulting from the division of the embryo sac mother cell have been described by other authors, but in the stages immediately following we are

confronted with a series of changes leading to a method of embryo sac formation quite different from any which has been hitherto described.

The cell walls which separate the four megaspores break down and disappear. Immediately following the formation of four fully separated daughter cells and nuclei (*figs. 8, 11*) we find a stage in which the same four nuclei are seen occupying a large cell with no traces of cell walls separating them (*fig. 14*). The evidence of the disappearance of the walls between the megaspores is not based on scattered examples, selected from a large number of specimens, but on a large number of continuous series of stages taken from a single inflorescence.

Fig. 11 shows four cells fully separated by cell walls, while in the next older flower on the same shoot are found four nuclei in a common cavity (*fig. 14*). In *fig. 13* the cell walls formed by the second or homeotypic division have entirely disappeared, while a slight but distinct cleft, extending across the cell, shows the location of the wall formed between the nuclei in the first division.

A statistical examination of a number of racemes to determine the exact stage of development of the mother cell or its products in each ovule, gave very conclusive evidence of the continuity of these series. The following is a fair example of an average shoot of the proper age. In this shoot of nine flowers the youngest flower had mother cells in a stage later than synapsis. The next older flower contained mother cells in the prophase and metaphase stages of the first division. The third showed in one ovule a heterotypic anaphase stage, and the other ovules showed the heterotypic telophase stages. The fourth flower showed the earlier stages of the second or homeotypic division. The fifth contained daughter nuclei of the second division in the telophase stage, and the sixth showed nuclei of this division separated by cell walls. The next older flower showed in a part of its ovules the four nuclei still separated by cell walls, while the rest of its ovules showed little or no trace of cell walls between the four nuclei. The ninth flower, the oldest on the raceme, showed four-celled embryo sacs in all its ovules, with no traces of cell wall separating the nuclei. The series here described shows no trace of the growth of one megaspore at the expense of the other three, or of the

first and second divisions of such a megaspore to form a four-celled embryo sac. We must conclude, therefore, that the walls between the four megaspores break down, and their nuclei become the first four nuclei of the embryo sac.

In the succeeding stages there is a continuous growth of the nuclei resulting from the reduction divisions and of the embryo sac formed from these nuclei. Very soon after the cell walls have disappeared from between the reduction nuclei, vacuoles begin to appear in the young embryo sac. *Figs. 15, 16, 17* illustrate the gradual enlargement of the cell containing the four nuclei, and the appearance of vacuoles in the cytoplasm. The vacuolization more than keeps pace with the enlargement of the embryo sac, and finally the separate vacuoles unite to form one large centrally located vacuole. It is at about this stage of growth that the third division takes place, forming the eight nuclei of the complete embryo sac (*fig. 17*). The embryo sac still continues to enlarge. The nuclei remain unchanged for a relatively long period. The polar nuclei come together and lie in contact during this period of quiescence, but are seen to be fused before the cells in the micropylar region show any signs of differentiation to form the egg apparatus. Not until nearly time for pollination is there any rearrangement of these cells, which are to form the egg apparatus.

When finally differentiated the synergids are pear-shaped and faintly striated. The egg is somewhat larger than the synergids, and usually has a large vacuole in the basal region. It stains less heavily than the synergids. I shall not here discuss the formation of the cell boundaries of the synergids and the egg. The antipodal nuclei are smaller than the others, and usually occupy a constricted region at the lower end of the embryo sac. These antipodal nuclei at this stage often number more than three, and in such cases are usually separated by division walls.

The most natural interpretation of the phenomena just described is that the first four cells formed by the division of the embryo sac mother cell are megaspores, and that these four spores jointly combine to form one embryo sac. It would seem that this assumption is the only one possible, for before the division membranes disappear, the four cells conform to all the criteria for spores in other similar

cases, and the mere loss of the division membranes cannot affect their morphological value.

Some preliminary studies of *Smilacina racemosa* seem to show that the two outer nuclei, formed in the double division of the embryo sac mother cell, undergo two further divisions to form the eight nuclei of the mature embryo sac. I shall describe this species, with other related species, more fully in a later paper.

Recent studies have brought to light an increasing number of so-called atypical methods of embryo sac formation, which must be considered in attempting its phylogenetic interpretation.

In Eichhornia, according to SMITH (22), a cell plate is rarely formed between the two nuclei resulting from the first division of the embryo sac mother cell, and a cell plate is also rarely formed between the daughter nuclei of the second division. Reduction takes place and one of the four megaspores forms the embryo sac.

CAMPBELL (2, 3) reported the discovery of the 16-nucleate embryo sac of *Peperomia pellucida*, and in the following year JOHNSON (13), working independently, published an account of the same species. The embryo sac mother cell develops directly into the embryo sac. The sixteen nuclei organize to form an embryo sac with an egg apparatus consisting of an egg and one synergid. Six nuclei are cut off singly around the periphery of the embryo sac, and the remaining eight nuclei fuse to form the endosperm nucleus. Later JOHNSON (14) reported that in *Peperomia hispidula* fourteen out of the sixteen nuclei of the embryo sac unite to form the endosperm nucleus.

In contrast with the large number of nuclei in the embryo sac of *Peperomia*, is the embryo sac of *Helosis guayanensis*, which is reported by CHODAT and BERNARD (7) to contain only four nuclei when mature. This 4-nucleate embryo sac is due to the disintegration of the lower nucleus of the first embryo sac division, so the products of the division of the upper nucleus alone enter into the embryo sac structure.

Avena fatua has been shown by CANNON (5) to form its megaspores similarly to Eichhornia. Commonly no cell walls are formed between the four spore nuclei, but the lower of these nuclei develops into the embryo sac and the other three degenerate.

A case resembling that of *Avena* and *Eichhornia* is reported as

occurring in *Crucianella* by LLOYD (15). He reports that in three species of *Crucianella* investigated, four megaspores were formed which were not separated by cell walls, and that "only occasional exceptions could be found to this." The *upper* of these four nuclei develops into the embryo sac, and the three lower finally degenerate. Not uncommonly these three lower nuclei undergo division. Many cases were seen, LLOYD reports, in which the four megaspores had each divided once, thus forming eight nuclei in a common cavity. He says: "If these divisions are regarded as the first mitoses of an embryo sac we have four embryo sacs lying tandem." Only the one lying adjacent to the micropyle attains full development. Although he reports the disintegration of the lower megaspores, his figures admit other interpretations. As late as the third division of the functional megaspore, what he interprets to be one of the three lower megaspore nuclei is shown dividing in the same cavity with the four dividing nuclei of the embryo sac. The dividing nuclei seem to have the same appearance in every way. This would certainly show a prolonged activity on the part of these three inner megaspores. This delayed germination of the lower megaspores and the similarity of the dividing nuclei in every way, open up many possibilities. The exact fate of the eight free nuclei formed by the division of all four of the megaspores is left unsettled. LLOYD concludes that the outer megaspore attains full development, and that the eight nuclei therefore never organize to form an embryo sac jointly. This is a most interesting case, and a complete history of the embryo sac from the mother cell may throw light on the interpretation of multinucleate embryo sacs.

This omission of the division walls between the megaspores of a tetrad is found by LLOYD also in *Asperula*, which is related to *Crucianella*. Any one of four spores may germinate to form the embryo sac, and the other three finally degenerate. The three spores which do not germinate are at times difficult to distinguish from antipodal nuclei.

An important conclusion to be derived from the behavior of *Eichhornia*, *Avena*, *Crucianella*, and *Asperula* is that the division walls are not essential to the individualization of a spore, and that the failure to form division walls between the megaspores does not

necessarily result in the lily type of embryo sac, even though the nuclei seem to be of the same size and vitality. So long as the spore retains its individuality as such, we can expect each spore to develop into a separate gametophyte, and not till this individuality is lost can we expect to find more than one spore entering into the structure of a single gametophyte. This absence of division walls, however, may very well lead directly to such joint organization of a gametophyte as we find in *Smilacina*.

LLOYD, in discussing the nature of the first four nuclei of the embryo sac of the lily, is in favor of calling them spores. "But after all," he says, "spores in the sense meant here are equivalent to vegetative cells of a somewhat special sort, with no necessarily separate existence teleologically speaking." He urges against the idea that in the lilies the gametophyte begins with the mother cell this: "It would seem more natural to regard the gametophyte as an individual by coalescence, having its origin in four like vegetative cells whose primitive function has been lost."

In *Pandanus Artocarpus* and *P. odoratissimus*, according to CAMPBELL (4), the mother cell develops directly into the 14-nucleate embryo sac. The two outer nuclei formed by the reduction divisions do not divide, while the two inner nuclei divide to form twelve nuclei. A differentiation of the antipodal cells was reported, but no certain evidence of nuclear fusions to form the endosperm nucleus was found.

In 1907 PORSCH (20) proposed the theory that the two cell groups in the opposite ends of the angiosperm embryo sac are both to be interpreted as archegonia. The synergids are thought to correspond to two neck canal cells, and the upper polar nucleus to the ventral canal cell of the archegonium. According to this theory the embryo sac of *Helosis* consists of only one archegonium, the other having been suppressed. The behavior of *Smilacina stellata* perhaps supports this theory, in so far as it shows the equivalent origin of the two groups of nuclei which PORSCH interprets as archegonia.

Miss PACE (19) has reported that *Cypripedium* forms a four-celled embryo sac by two divisions of the lower of two "megaspores." This embryo sac may be interpreted by PORSCH's theory to be a single archegonium.

WENT (28), in a recent article on the Podostemaceae, reports that

in *Oenone* and *Mourera* a four-celled embryo sac is formed, similar to that in *Helosis*. The mother cell following synapsis divides to form two daughter cells, the upper degenerating. The lower daughter cell (which he calls the "megaspore") divides, and the innermost nucleus shrinks immediately to a shapeless mass of chromatin that is visible for a long time. This inner nucleus, though one of the first four nuclei formed by the division of the embryo sac mother cell, is interpreted by WENT as a nucleus of the embryo sac and not a spore. The nucleus remaining from the second division divides twice to form the four-celled embryo sac. The lower nucleus of this embryo sac degenerates, leaving only the three nuclei which form the egg apparatus. WENT notes that his results support the theory of PORSCH, except that the ventral canal cell is on the wrong side of the egg.

ERNST (10) has expressed the opinion that the 16-nucleate embryo sac of *Gunnera*, as described by him, consists of two of the archegonia of PORSCH in the chalazal end of the embryo sac and one in the micropylar end. Four nuclei in the central region of the embryo sac fail to form an archegonium, and unite with a polar nucleus from each archegonium to form the endosperm nucleus.

STEPHENS (23), in a preliminary note on certain *Penaeaceae*, reports that the sixteen nuclei of the embryo sac become divided into four groups, which lie at some distance from one another against the wall of the embryo sac. Three nuclei out of each group of four organize what appears to be an egg apparatus, while one nucleus from each group acts as a polar nucleus, and the four unite to form the endosperm nucleus. On PORSCH's theory these four groups would represent four archegonia.

These examples seem to indicate a tendency of the nuclei of the angiosperm embryo sac to form groups of four. The evidence in favor of the archegoniate character of these groups, however, seems to me to be insufficient as yet. The relationship between the angiosperms and the gymnosperms is so remote that a comparison of the embryo sacs of the two groups with a view to homologizing the groups of nuclei associated with the egg is very difficult.

COULTER (8) further defends the idea that the first four nuclei of the embryo sac of the lily are megaspores, or "at least their nuclei."

His evidence lies in the fact of their being the product of the two reduction divisions. Hence they must be "megaspore nuclei, to be recognized as such by their cytological history and structure." The 16-nucleate embryo sacs of *Peperomia pellucida* are considered as resulting from two divisions of each of these megaspore nuclei, and the 8- and 16-nucleate embryo sacs, which JOHNSON reports as occurring in *Peperomia hispidula*, are regarded as formed by one division of each of the four megaspore nuclei to form the 8-nucleate embryo sac, and by two divisions of each to form the 16-nucleate embryo sac.

COULTER is inclined to regard it as a fundamental law that the angiosperm embryo sac is formed from the mother cell by never more than five nuclear divisions, the reduction divisions and three divisions of a megaspore. He concludes that the large number of nuclei in the embryo sacs of *Peperomia* and *Pandanus* may originate by the participation of more than one spore in their organization. This implies, further, that any embryo sac formed from one spore which has sixteen or more nuclei can be considered as relatively primitive, since it would require more than five nuclear divisions to produce it from the mother cell.

I do not see why the cases of the proliferation of antipodal nuclei should not be given more weight in the evidence. There is certainly an abundance of cases among the grasses and in the Ranunculaceae, as well as in other families, in which the innermost nuclei of the embryo sac are the product of more than five divisions previous to fertilization. It seems doubtful whether the embryo sac with more than eight nuclei can be explained on any such simple hypothesis, and it is to be remembered that, while there is apparently a physiological necessity back of the double division, there is nothing, as STRASBURGER has noted, in the phylogeny of the angiosperms which would explain or give special significance to a fivefold division.

BROWN (1) reports that evanescent cell walls are formed separating the first four nuclei of the embryo sac of *Peperomia Sintensii* and *P. arifolia*, in both of which the mother cell develops directly into the embryo sac. Though evidently convinced that in *Peperomia* these first four nuclei are megasporangia, BROWN seems to object to the adoption of this explanation for the lily type of embryo sac in general.

Referring to the number of divisions which archesporial cells undergo to form the mother cell, he says: "Since we can trace the reduction of these divisions until, among the angiosperms, the archesporial cell may, without dividing, form one megaspore mother cell, it does not seem reasonable to suppose that the divisions of the mother cell to form four megasporocytes may not also be left out, and the mother cell function directly as a megaspore." Any analogy, however, based upon the archesporial cell, has against it that this latter cell is a doubtful morphological unit.

It cannot be maintained that any morphological interpretation yet proposed satisfactorily explains all the diverse types of embryo sac formation which have been described. That there are so many variations in important particulars gives ground for the expectation that further study may fill up many gaps in our current interpretations.

It is plain that within the group of the Convallariaceae there are types which go far toward explaining the origin of the old and familiar lily type of embryo sac. It is certainly plain that in *Smilacina stellata* four megasporocytes are formed, which are unmistakably separated by cell walls and subsequently recombine to form the first four nuclei of the embryo sac.

All the evidence favors the view that the first four nuclei of the lily embryo sac are morphologically, as well as from the standpoint of the reduction divisions, to be interpreted as megaspore nuclei.

SUMMARY

1. The mother cell of *Smilacina stellata* divides twice to form four nuclei, which are separated by walls to form four megasporocytes.

2. The division walls and plasma membranes which separate the four nuclei are absorbed, so that the four reduction nuclei occupy a common cell cavity.

3. Each of these four nuclei divides again, and the resulting eight nuclei organize to form the embryo sac.

4. It is plain from these facts that we have four individual megaspore cells combining to form one embryo sac or gametophyte in *Smilacina stellata*.

5. It is thus strongly suggested that in the embryo sac of the lilies the first four nuclei are morphologically megasporocytes.

6. In *Smilacina racemosa* the outer daughter cell of the heterotypic division develops into the embryo sac, although the long persistence of the two nuclei formed by the division of the inner heterotypic nucleus might suggest that they should be considered a part of the embryo sac. *Smilacina racemosa* shows temporary cell division at the close of the homeotypic division, agreeing in this respect with *Smilacina stellata*.

I wish to express my obligations to Professor H. D. DENSMORE, in whose laboratory at Beloit College this investigation has been largely carried on. I am also indebted to Professor R. A. HARPER for his suggestions and criticisms during the preparation of the manuscript.

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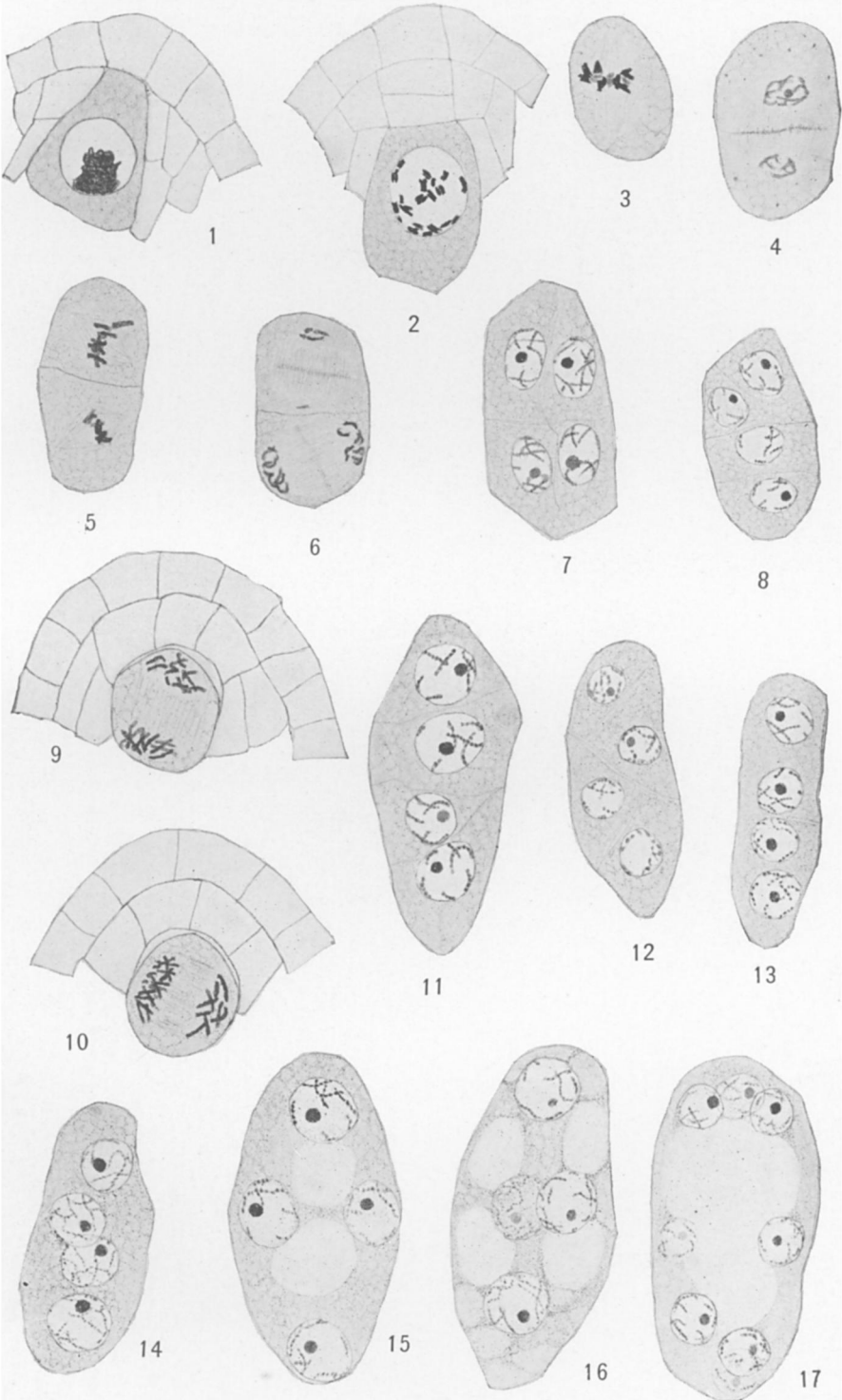
EXPLANATION OF PLATE XV

All figures were drawn with the aid of a camera lucida. The magnification in all the drawings is 670 diameters. The micropylar end is upward in each drawing.

FIG. 1.—Mother cell in synapsis stage; without tapetal cell.

FIG. 2.—Mother cell in prophase stage of first division; two cell layers between the epidermis and the mother cell.

FIG. 3.—Early metaphase stage of the mother cell, showing thick double chromosomes characteristic of first reduction division.



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FIG. 4.—Formation of cell plate and daughter nuclei at the close of first division of mother cell.

FIG. 5.—Early metaphase stage of homotypic division; axes of spindles oblique.

FIG. 6.—Daughter nuclei and cell plates forming at the close of second division; outer daughter cell dividing transversely and inner one longitudinally.

FIG. 7.—Nuclei of second division fully formed, arranged bilaterally; division membranes of second division do not reach outside walls.

FIG. 8.—The outer daughter cell has divided longitudinally and the inner one transversely.

FIGS. 9, 10.—Two successive sections of the same nucellus, showing the division of an approximately spherical mother cell; heterotypic division longitudinal; one daughter cell in the homeotypic division dividing longitudinally and the other transversely.

FIG. 11.—Row of four very large megaspores, with the division walls very indefinite.

FIG. 12.—Commonest arrangement of megaspores, in which first division is oblique and second at right angles to first; walls have disappeared but plasma membranes still persist.

FIG. 13.—Four megaspores; a cleft between two middle nuclei is all that remains of division membranes of cells.

FIG. 14.—Four megaspores, with no traces of cell walls, forming four-celled stage of embryo sac.

FIGS. 15, 16.—Stages in the vacuolation of the four-celled embryo sac.

FIG. 17.—Eight-celled embryo sac, showing micropylar and antipodal groups of nuclei, the two polar nuclei already separated out.